Behavioral/Cognitive

Lateral Orbitofrontal Cortex Links Social Impressions to Political Choices

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Recent studies of political behavior suggest that voting decisions can be influenced substantially by "first-impression" social attributions based on physical appearance. Separate lines of research have implicated the orbitofrontal cortex (OFC) in the judgment of social traits on the one hand and economic decision-making on the other, making this region a plausible candidate for linking social attributions to voting decisions. Here, we asked whether OFC lesions in humans disrupted the ability to judge traits of political candidates or affected how these judgments influenced voting decisions. Seven patients with lateral OFC damage, 18 patients with frontal damage sparing the lateral OFC, and 53 matched healthy participants took part in a simulated election paradigm, in which they voted for real-life (but unknown) candidates based only on photographs of their faces. Consistent with previous work, attributions of "competence" and "attractiveness" based on candidate appearance predicted voting behavior in the healthy control group. Frontal damage did not affect substantially the ability to make competence or attractiveness judgments, but patients with damage to the lateral OFC differed from other groups in how they applied this information when voting. Only attractiveness ratings had any predictive power for voting choices after lateral OFC damage, whereas other frontal patients and healthy controls relied on information about both competence and attractiveness in making their choice. An intact lateral OFC may not be necessary for judgment of social traits based on physical appearance, but it seems to be crucial in applying this information in political decision-making.

Key words: **decision-making; frontal lobes; human; neuropolitics; neuropsychology; social neuroscience**

Introduction

Rightly or wrongly, we form impressions about other people based on appearance. This ranges from assessment of traits that are related directly to appearance, such as attractiveness (Thornhill and Gangestad, 1999; O'Doherty et al., 2003; Winston et al., 2007), to inferences about personal characteristics, such as intelligence, warmth, or neuroticism (Berry, 1989; Zebrowitz et al., 2002; Bar et al., 2006; Penton-Voak et al., 2006; Little and Perrett, 2007). Although inferences based on appearance can be inaccurate (Olivola and Todorov, 2010), first impressions nonetheless can strongly influence social decision-making (Hassin and Trope, 2000; Bhanji and Beer, 2013).

In democracies, voting is one of the essential political acts that citizens undertake. In principle, voting is a complex judgment, requiring deliberation about the candidates' party affiliation, as well as their policy positions, personal attributes, and past record (Lewis-Beck et al., 2008). However, in practice, information inferred from appearance alone may influence substantially voters' choices: recent work has shown that competence ratings inferred solely from campaign photographs predict the winners of real elections (Todorov et al., 2005; Antonakis and Dalgas, 2009). Understanding the brain mechanisms underlying these first-impression effects on voting is one route to a deeper understanding of human political behavior and offers a novel perspective on the broader topic of value-based decision-making, to date studied mainly through an economic lens (Rangel et al., 2008; Padoa-Schioppa, 2011).

The ventral frontal lobe, encompassing the medial and lateral orbitofrontal cortex (LOFC) and ventromedial prefrontal cortex (vmPFC), has been implicated in value-based decision-making in economic paradigms (Fellows, 2007; Camille et al., 2011; Grabenhorst and Rolls, 2011), including when integration across multiple attributes is required (Fellows, 2006; Kahnt et al., 2011). It has also been linked to the assessment of social information from photographs or videos (O'Doherty et al., 2003; Willis et al., 2010; Tsuchida and Fellows, 2012; Bhanji and Beer, 2013), including the judgment of beauty (or esthetic value) in faces (Pegors et al., 2015).

Within this broad region, the LOFC is of particular interest. Recent fMRI studies found that activity in this region scales with

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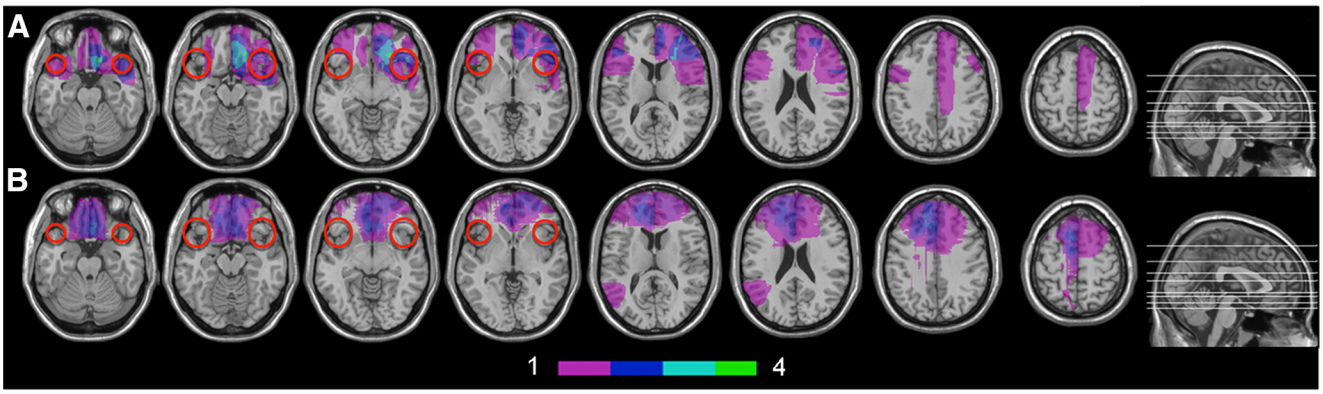

Figure 1. Lesion overlap is shown for subjects with damage affecting the LOFC (LOFC group) (***A***) or areas of the frontal lobe sparing the LOFC (FC group) (***B***) on the same axial and sagittal views of the MNI brain. The number of subjects with damage affecting a given voxel is indicated by the color, as shown in the legend. The LOFC region of interest applied to assign patients to these groups is shown by the red circle.

first impressions in social judgment tasks (Kim et al., 2012; Bhanji and Beer, 2013). This may reflect a general role for this region in dynamic, context-sensitive assignment of value to visual stimuli: selective lesions in the homologous region in macaques (Wallis, 2012) disrupt learning the value of abstract stimuli within a particular context (Noonan et al., 2010; Walton et al., 2010). Electrophysiological work in the same species is consistent with the LOFC representing the value of a particular (visual) stimulus (Rich and Wallis, 2014). Although it has been shown that ventral frontal damage in humans changes how information is gathered in economic multi-attribute decision-making (Fellows, 2006) and impairs interpretation of subtle social information (Beer et al., 2006; Willis et al., 2010; Tsuchida and Fellows, 2012), it is not clear whether shared brain mechanisms underlie these observations. No human lesion studies to date have considered decision-making in a sociopolitical context, and very few have focused on the LOFC in particular in any context. Here, we test the effects of LOFC damage in humans on a political choice task, asking whether this region is critical for judging social attributes from faces, for applying that information to make voting decisions, or both.

Materials and Methods

Subjects. Twenty-five patients with focal frontal lobe damage suffered at least 6 months before testing were recruited through the cognitive neuroscience research databases of McGill University and the University of Pennsylvania. Lesions were characterized by computerized tomography or magnetic resonance imaging and registered manually to the standard Montreal Neurological Institute (MNI) brain using MRIcro software by a neurologist experienced in this procedure (L.K.F.) and blind to task performance. The same software was used to create lesion overlap images and estimate lesion volumes.

The primary region-of-interest analysis focused on the LOFC, defined as any lesion that overlapped with a 17-mm-radius sphere centered on MNI (x, y, z) coordinates (± 42, 20, -10). These coordinates were based on the BOLD activation peak related to dynamic positive social evaluation reported in a recent fMRI study of social impression formation (Bhanji and Beer, 2013). Seven patients with damage overlapping this region of interest in either hemisphere were assigned to the LOFC group. The remaining 18 were assigned to the frontal lobe-lesioned control (FC) group. LOFC lesions were restricted to the right hemisphere in five cases and left hemisphere in two cases; FC lesions affected the left hemisphere in 10 patients, the right hemisphere in five patients, and both hemispheres in three patients. Lesions in the LOFC groups included three cases of ruptured cerebral aneurysms, three tumor resections, and one ischemic stroke. The FC group included six cases of ruptured aneurysm, eight tumor resections, and four ischemic strokes. Seven FC patients and two LOFC patients were taking one or more psychoactive medications. These were most commonly antidepressants or anticonvulsants. There was no significant difference in lesion volume ($t_{(23)} = -0.981$, $p = 0.34$), lesion etiology (vascular vs tumor, $\chi^2_{(1,25)} = 0.005$, $p = 0.94$), or use of psychoactive medication ($\chi^2_{(1,25)} = 0.233$, $p = 0.63$) between the FC and LOFC groups. Figure 1 shows the lesion overlap images for these two groups.

Table 1. Demographic and background information for all three groups [mean (SD)]

Group	Age (years)	Education (years)	Gender (males/females)	BDI	Lesion volume (cm^3)
HC ($n = 53$)	56.1 (12.3)	15.1 (2.4)	20/33	2.09 (3.22)*	
FC ($n = 18$)	57.4 (11.3)	14.9 (2.0)	8/10	9.39 (10.70)	36 (52)
LOFC ($n = 7$)	56.7 (14.1)	16.9 (2.5)	3/4	10.14 (6.41)	60 (61)

*$p < 0.05$, HCs differed significantly from both frontal groups (ANOVA).

In a secondary analysis, we tested a second, more standard region of interest, classifying patients based on whether the medial OFC and/or vmPFC was involved (VMF group, $n = 13$) or spared (NVMF group, $n = 12$), following boundaries laid out previously (Stuss and Levine, 2002), as in our previous studies of value-based decision-making (Fellows and Farah, 2007; Camille et al., 2011). Of the seven LOFC patients, four were reclassified as VMF and three as NVMF; of 18 FC patients, nine were reclassified as VMF and nine as NVMF. To interpret that result, we also explored the performance of patients in the VMF group with lesions restricted to the medial OFC/vmPFC (i.e., sparing the LOFC) compared with a control group with frontal damage sparing both the medial OFC/vmPFC and LOFC.

We recruited 53 healthy controls (HCs) through advertisement in the community, matched for age ($F_{(2,75)} = 0.08$, $p = 0.92$) and education ($F_{(2,75)} = 2.04$, $p = 0.14$). All groups included a similar proportion of males and females ($\chi^2_{(2,78)} = 0.28$, $p = 0.87$). The HCs were free of neurologic or psychiatric illness, had no history of significant head injury, and were not taking psychoactive medication. HCs scored <14 on the Beck Depression Inventory (BDI) and ≥ 26 on the Montreal Cognitive Assessment. As is typically observed in neurological populations, both frontal groups scored significantly higher on the BDI than HCs ($F_{(75,2)} = 13.16$, $p < 0.05$). However, the two patient groups did not differ from each other ($t_{(23)} = -0.17$, $p = 0.86$). No frontal patient suffered from active depression at the time of testing according to the referring physician, confirmed by patient self-report. Background demographic information is presented in Table 1. Patient groups did not differ in performance on the common set of screening neuropsychological tests (Table 2).

All participants provided written informed consent in accordance with the principles of the Declaration of Helsinki and the stipulations of the local institutional review boards. Participants were paid a nominal fee for their time and inconvenience, and travel costs were reimbursed.

Table 2. Performance on selected screening tests for the two patient groups [mean (SD)]

Group	Digit span forward	Digit span backward	Animal fluency	F fluency	A fluency	S fluency
FC	5.83 (1.03)	4.35 (1.17)	17.4 (3.6)	10.3 (4.7)	10.4 (4.4)	11.6 (5.7)
LOFC	6.25 (0.96)	4.67 (1.63)	17.2 (4.2)	9.5 (7.1)	11.2 (6.6)	12.6 (6.9)

Not all subjects completed all tests. Groups did not differ on any of these measures (*t* test, $p > 0.05$).

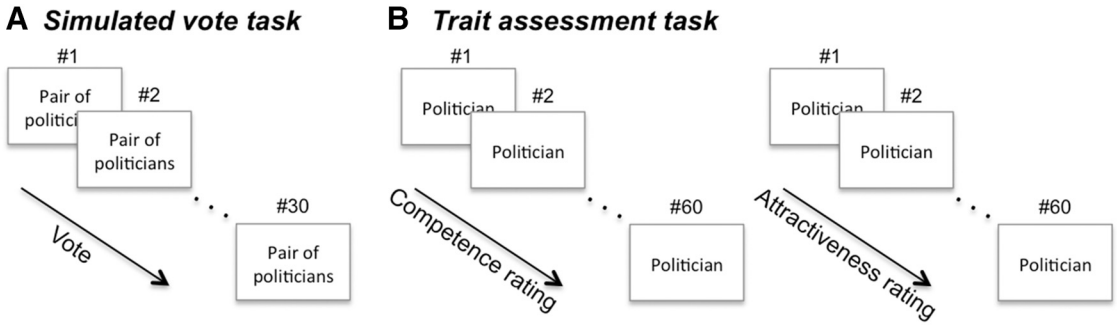

Figure 2. Outline of the experimental procedure: participants first chose their preferred candidate in each of 30 pairs of political opponents shown for 2 s, with an unlimited response window, in the simulated vote task (***A***). After completion of additional tasks that served as distractors for the purpose of this study, they then rated all 60 candidates, viewed one by one, on perceived competence and attractiveness in the trait assessment task (***B***). The order of trait assessment was randomized across participants. No time limit was set for individual trials in either task, but participants were encouraged to rely on their first impressions and to give their response as rapidly as possible.

Tasks. We used 60 grayscale head-and-shoulder images of political candidates, 30 pairs of opponents in actual elections for the U.S. House of Representatives or Senate in 2000, 2002, or 2004, a subset of stimuli from previous work (Todorov et al., 2005; Spezio et al., 2008; Olivola and Todorov, 2010). All tasks were administered with E-Prime software.

Subjects began with the simulated vote task in which they were instructed to imagine participating in an election. They were shown 30 pairs of political candidates and asked to vote for a politician in each pair based solely on the photographs. Each pair of faces remained on the screen for 2 s. Subjects were encouraged to rely on their "first impressions" and to choose as rapidly as they could. Both the order of the pairs and the left–right position of faces within each pair were randomized across subjects. This voting task was followed by several additional tasks unrelated to the present study, serving as distractors for the purposes of this experiment. Participants were then asked to rate each of the 60 faces, presented one at a time, on how competent and attractive each appeared to be in the trait assessment task. Trait ratings were made on a scale of 1 to 10, with 1 indicating "not at all" and 10 indicating "extremely." All 60 faces were first rated for one trait and then presented again for rating of the second trait. The order of the two trait rating tasks and the order of individual faces within each trait rating block were randomized across subjects. Although no time limit was set, subjects were encouraged to perform the ratings quickly. Figure 2 depicts trial events in both tasks. At the end of the entire experimental session, participants were asked whether they had recognized any of the faces from previous exposures (e.g., in the media). None of the political candidates was recognized by any participant.

Data analysis. To assess subjects' judgment of social traits from faces, we calculated subjects' average ratings across all 60 faces for each trait and compared group means using one-way ANOVA. We similarly tested for group differences in social trait judgments of individual faces using one-way ANOVA to compare trait ratings across the three groups for each face.

Logistic regression was used to compare the degree to which trait ratings predicted simulated vote decisions across all three groups. We created two dummy variables, one for FC patients and one for LOFC patients, with HCs serving as the reference category. We then constructed interactions between these dummy variables and the differences in trait ratings for each pair of candidates. Whether the candidate presented on the left side of the screen was chosen served as the dependent variable. Given the violation of the assumption of independent error terms, the analyses were clustered within subjects. To facilitate comparison between the LOFC, FC, and HC groups, logistic regression models were used to estimate predicted probabilities. A secondary analysis repeated this procedure with the frontal group split according to alternative regions of interest, as described above.

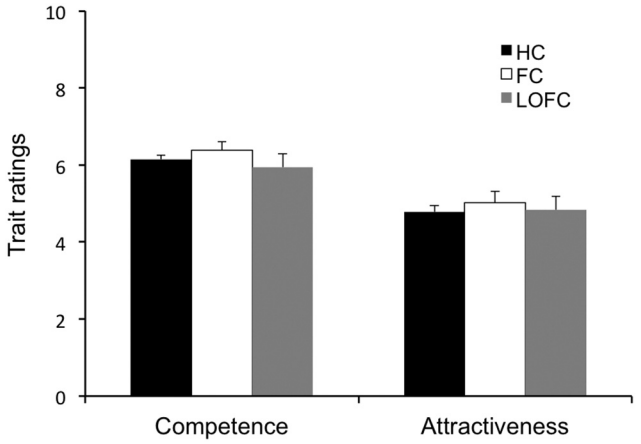

Figure 3. Mean competence and attractiveness ratings across all faces, by group. Error bars indicate SEM.

Results

Trait assessment

Groups did not differ in their average "competence" or "attractiveness" ratings for the stimulus set as a whole (ANOVA: competence, $F_{(2,75)} = 0.79$, $p = 0.45$; attractiveness, $F_{(2,75)} = 0.27$, $p = 0.77$; Fig. 3). There was also a high correlation between groups for both traits (mean competence ratings for HC vs LOFC, Pearson's $r = 0.81$, $p < 0.001$; mean attractiveness ratings for HC vs LOFC, $r = 0.84$, $p < 0.001$). We explored whether there were groupwise differences in the ratings of individual faces: of 60 faces, a significant group difference in competence ratings was found for only four faces ($F_{(2,76)} = 4.69$, $F_{(2,76)} = 4.58$, $F_{(2,76)} = 3.32$, $F_{(2,76)} = 5.02$, p values ranging from 0.009 to 0.04, uncorrected); for attractiveness ratings, a significant group difference was found for only one face ($F_{(2,76)} = 3.57$, $p = 0.03$); none of these effects survive Bonferroni's correction. Competence and attractiveness ratings were also correlated across the stimulus set in all three

Table 3. Influence of trait rating difference on candidate choice for the FC and LOFC groups, with the HC group serving as the reference

	Model [OR (95% CI)]		
	Competence	Attractiveness	Full
Group (vs HC)			
FC	0.85 (0.63–1.14)	0.84 (0.63–1.12)	0.84 (0.63–1.14)
LOFC	1.12 (0.85–1.46)	1.09 (0.84–1.42)	1.08 (0.82–1.43)
Competence rating difference	1.25 (1.16–1.34)***		1.16 (1.09–1.24)***
FC × competence rating difference	0.96 (0.85–1.08)		0.99 (0.89–1.11)
LOFC × competence rating difference	0.82 (0.74–0.92)**		0.86 (0.77–0.96)**
Attractiveness rating difference		1.32 (1.22–1.43)***	1.27 (1.18–1.37)***
FC × attractiveness rating difference		0.91 (0.80–1.02)	0.91 (0.81–1.02)
LOFC × attractiveness rating difference		0.95 (0.80–1.12)	0.99 (0.83–1.17)
Constant	0.90 (0.80–1.01)[a]	0.92 (0.81–1.04)	0.93 (0.82–1.06)
Number of observations	2321	2321	2321

HCs were significantly more likely to choose the candidate they perceived as more competent or attractive, as indicated by ORs significantly >1 for "Competence rating difference" and "Attractiveness rating difference." LOFC patients were significantly less likely than HCs to choose the candidate they perceived as more competent, as indicated by ORs <1 for "LOFC × competence rating difference." LOFC patients were as likely as HCs to choose based on difference in perceived attractiveness, as indicated by ORs not different from 1 for "LOFC × attractiveness rating difference." The pattern of the results is the same whether competence and attractiveness were entered in separate or the same regression models.
**$p < 0.01$, ***$p < 0.001$, [a]$p < 0.1$.

groups, to a similar degree (HCs, Pearson's $r = 0.46$, $p < 0.001$; FC patients, $r = 0.35$, $p < 0.001$; LOFC patients, $r = 0.36$, $p < 0.001$). These findings suggest that the groups do not differ systematically in their use of the rating scales, the ability to detect competence and attractiveness from faces, or the relationship between their judgment of these two attributes across stimuli.

Influence of trait assessment on vote choice

Next, we estimated logistic regression models to assess how perceived competence and attractiveness affected vote choices. We first examined the effect of competence ratings without adjusting for attractiveness ratings and vice versa in separate models. We then entered both ratings in a full model (Table 3). For HCs, the difference in competence rating between the two candidates in each race was related significantly to the choice of one candidate over the other [odds ratio (OR) = 1.25, 95% confidence interval (CI) = 1.16–1.34], i.e., for every one unit increase in the difference in competence ratings between a candidate and his or her opponent, the odds of choosing the more competent-appearing candidate increased by 25%. No significant interaction was found between FC patient status and competence rating difference ($p > 0.1$), indicating that competence ratings predicted candidate choices to a similar degree in FC patients and HCs. However, there was a significant interaction between LOFC patient status and competence rating difference ($p < 0.01$). That is, LOFC patients differed from HCs in how perceived competence affected vote choice. Competence rating differences were significantly less likely to influence the candidate choice of LOFC patients compared with HCs. Among LOFC patients, a one unit change in competence rating difference was associated with an OR of 1.03 (95% CI = 0.94–1.12), i.e., not different from chance, whereas among FC patients, a one unit change in competence rating difference was associated with an OR of 1.19 (95% CI = 1.09–1.31), above chance and indistinguishable from the HC group.

A different pattern was evident for the influence of perceived attractiveness on vote choice. As with competence, differences in attractiveness ratings were related significantly to vote choice for HCs (OR = 1.32, 95% CI = 1.22–1.43), but now both FC and LOFC patients were statistically indistinguishable from HCs (p values > 0.1). The absence of a significant interaction between attractiveness rating difference and FC or LOFC group indicates that the odds of both FC and LOFC patients choosing their preferred candidate based on difference in perceived attractiveness were indistinguishable from HCs.

We next assessed the effect of both competence and attractiveness rating differences and their associated interactions with patient groups in the same regression model to examine the simultaneous influence of perceived competence and attractiveness on vote choice. The main effects of competence and attractiveness rating difference on vote choice both remained highly significant in HCs (competence, OR = 1.16, 95% CI = 1.09–1.24; attractiveness, OR = 1.27, 95% CI = 1.18–1.37), suggesting that the influence of perceived competence and attractiveness on vote choice are relatively independent of one another. The similar ORs and overlapping CIs also indicate that the two had a similar magnitude of influence on vote choice, with attractiveness slightly more predictive. The interaction between competence rating difference and LOFC group also remained significant ($p < 0.01$). That is, the difference in competence rating had a different influence on the probability of choosing a given candidate in the LOFC group than in the HC group. In the HC group, every one unit change in competence rating difference was associated with an odds of choosing the more competent-appearing candidate of 1.16 (95% CI = 1.09–1.24), or a 16% higher odds of choosing that candidate. In the LOFC group, the difference in competence rating had no influence on the odds of choosing a given candidate (OR = 1.00, 95% CI = 0.92–1.09). There continued to be no statistically significant interaction between attractiveness rating difference and LOFC status ($p > 0.1$), confirming that the degree to which this group relied on attractiveness ratings was indistinguishable from the pattern in HCs.

Thus, whether the influences of trait judgments on voting choices are analyzed separately or together, the same pattern is evident: LOFC patients were significantly less likely than HCs to choose a candidate based on difference in perceived competence but were as likely to choose based on perceived attractiveness, whereas FC patients were as likely as HCs to choose a candidate based on differences in both perceived competence and attractiveness. These relationships are shown graphically in Figure 4, which illustrates the predicted probability of choosing one candidate over his or her opponent based on competence or attractiveness rating difference, based on the full model. These differences in how attribute ratings predicted choice after LOFC damage were not accompanied by reaction time differences; there

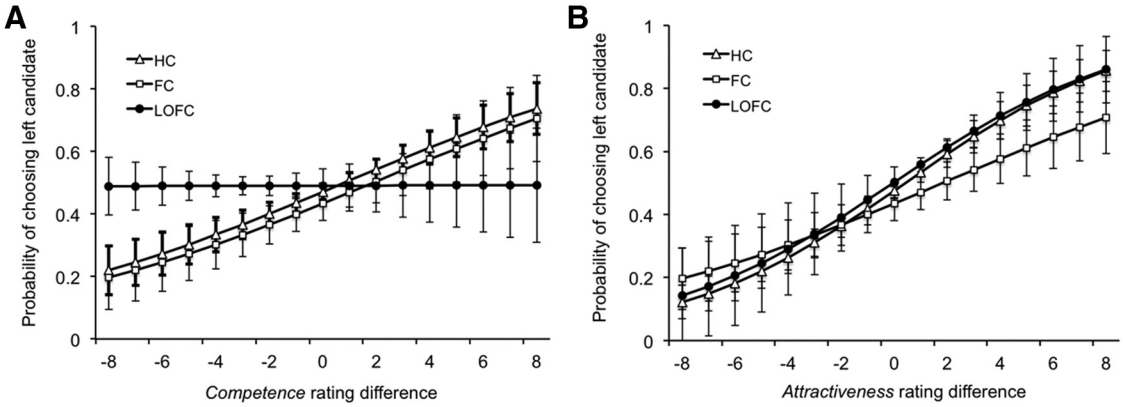

Figure 4. Predicted probabilities of choosing the candidate presented on the left side of the screen in relation to the difference in competence (***A***) or attractiveness (***B***) ratings between the two candidates in each trial (left–right), estimated with both traits entered in the same regression model. The horizontal axes range from −8 to 8 because the largest absolute difference recorded on the 1–10 scale was 8.

was no significant difference in choice reaction time across groups (ANOVA, $F_{(2,75)} = 1.8$, $p = 0.18$).

A similar logistic regression analysis was conducted using absolute trait ratings of all 60 individual faces instead of the trait rating difference for pairs of candidates as the predictor. Again, competence emerged as a significant predictor of candidate choice for FC patients and HCs but not for LOFC patients (results not shown), indicating that the present pattern of findings is robust to different specifications of the trait variables. Perceived attractiveness continued to have a significant effect for all three groups.

Trait ratings predicting simulated vote outcome in VMF versus NVMF patients

Our main hypothesis was that the LOFC plays a key role in relating social trait assessment to vote choice. However, many previous studies of patients with prefrontal lesions have used larger regions of interest, providing evidence that the ventromedial frontal lobe more generally is critical for particular aspects of value-based decision-making (Fellows, 2007; Camille et al., 2011; Grabenhorst and Rolls, 2011; Kahnt et al., 2011). The LOFC group studied here includes some individuals with damage extending into more medial frontal areas to varying degree and, in other cases, into the ventrolateral PFC. To relate the present finding to this previous literature and to provide evidence as to whether the behavioral effects are driven by damage to the LOFC or to adjacent areas, we performed a secondary analysis to explore the effect of orbitofrontal and/or ventromedial prefrontal lobe damage on the same behavioral measures. When the group was split into VMF ($n = 13$), NVMF ($n = 12$), and HC ($n = 53$) groups according to standard landmarks (see above), four LOFC patients were classified in the VMF group and three in the NVMF group. No difference was seen in average trait ratings across VMF, NVMF, and HC groups (ANOVA: competence, $F_{(2,75)} = 0.187$, $p = 0.83$; attractiveness, $F_{(2,75)} = 0.131$, $p = 0.88$). The same logistic regression modeling, with the HC group again serving as the reference category, showed that higher competence ratings predicted vote choices for the NVMF group to a similar degree as in the HC group (as indicated by the lack of any significant interaction between NVMF status and differences in competence ratings; $p > 0.1$). However, the interaction between VMF status and competence rating difference shows that perceived competence has significantly less influence on vote choices in VMF patients. Conversely, all three groups were equally likely to vote for the candidate with higher attractiveness rating, with no detectable difference in the extent to which perceived attractiveness influenced vote choice (p values > 0.1).

Table 4. Influence of trait rating difference on candidate choice for the NVMF and VMF groups, with the HC group as the reference

	Full model [OR (95% CI)]
Group (vs HC)	
NVMF	0.77 (0.54, 1.10)
VMF	1.04 (0.81, 1.35)
Competence rating difference	1.16 (1.09, 1.24)***
NVMF × competence rating difference	1.01 (0.87, 1.17)
VMF × competence rating difference	0.90 (0.81, 1.00)*
Attractiveness rating difference	1.27 (1.18, 1.37)***
NVMF × attractiveness rating difference	0.94 (0.82, 1.07)
VMF × attractiveness rating difference	0.93 (0.81, 1.07)
Constant	0.93 (0.82, 1.06)
Number of observations	2 321

HCs were significantly more likely to choose the candidate they perceived as more competent or attractive, as indicated by ORs significantly >1 for "Competence rating difference" and "Attractiveness rating difference." VMF patients were significantly less likely than HCs to choose the candidate they perceived as more competent, as indicated by ORs <1 for "VMF × competence rating difference." VMF patients were as likely as HCs to choose based on difference in perceived attractiveness, as indicated by ORs not different from 1 for "VMF × Attractiveness rating difference." * $p < 0.05$, *** $p < 0.001$.

This contrasting pattern of the influence of perceived competence and attractiveness was preserved when competence and attractiveness ratings were assessed in a single logistic regression model, indicating that these two traits influence vote choice independently and that the different pattern seen in the VMF group is particular to competence ratings. Taking the significant interaction into account, the OR for the VMF group choosing the candidate with the higher competence rating is 1.05 (95% CI = 0.97–1.13), indicating that the voting of the VMF group was not influenced by perceived competence. Table 4 summarizes these results.

Overall, the pattern in the VMF group is similar to that seen in the more narrowly defined LOFC group. Both LOFC and VMF groups were as likely as HCs to choose based on attractiveness ratings. Both groups were also less likely to choose a candidate based on previous ratings of competence. However, the point estimate for the ORs for the influence of competence rating on choice is farther from 1.00 in VMF patients compared with LOFC patients, suggesting the possibility that the loss of the influence of competence on voting is more strongly related to LOFC damage

Table 5. Influence of trait rating difference on candidate choice for NVMF (excluding the LOFC) patients and vmPFC/OFC (i.e., VMF group excluding the LOFC) patients, with the HC group serving as the reference

	Full model [OR (95% CI)]
Group (vs HC)	
NVMF (excluding LOFC cases)	0.66 (0.45, 0.98)*
vmPFC/OFC (excluding LOFC cases)	1.05 (0.74, 1.48)
Competence rating difference	1.16 (1.09, 1.24)***
NVMF × competence rating difference	1.04 (0.90, 1.22)
vmPFC/OFC × competence rating difference	0.96 (0.84, 1.10)
Attractiveness rating difference	1.27 (1.18, 1.37)***
NVMF × attractiveness rating difference	0.94 (0.82, 1.06)
vmPFC/OFC × attractiveness rating difference	0.89 (0.77, 1.02)[a]
Constant	0.93 (0.82, 1.06)
Number of observations	2 111

Competence and attractiveness rating differences were related significantly to candidate choice in HCs. Patients with damage to the vmPFC/OFC sparing the LOFC and patients with damage to other frontal areas sparing the LOFC were as likely as HCs to choose based on perceived competence and attractiveness, as indicated by the lack of interaction between trait rating differences and either patient group status. *$p < 0.05$, ***$p < 0.001$, [a]$p < 0.1$.

than to VMF damage in general. To more directly test that claim, we examined the effect of VMF damage that affected only medial vmPFC/OFC, i.e., sparing the LOFC (vmPFC/OFC, $n = 9$) on the same measures, compared with a frontal control group from which we excluded all LOFC patients (NVMF excluding the LOFC, $n = 9$). With the full HC group as the reference, there was no significant interaction between competence rating difference and patients with vmPFC/OFC damage sparing the LOFC, indicating that this damage did not substantially affect the influence of competence rating on voting choice ($p > 0.1$; Table 5). This provides preliminary evidence that the lack of influence of perceived competence on vote choice seen in the group with LOFC damage, and also detectable in the broader VMF group, is likely driven by LOFC damage.

Discussion

This is the first study of the effects of frontal lobe damage on political decision-making. We focused on a very restricted form of political choice: voting based on appearance alone. Voting based on superficial first impressions has been shown to predict real electoral outcomes, suggesting that the processes underlying these decisions are ecologically important (Todorov et al., 2005; Antonakis and Dalgas, 2009). Even in this information-poor context, participants readily distinguished candidates in terms of physical attractiveness and drew inferences about their competence. Judgments of both traits have been shown previously to predict either real life (Ballew and Todorov, 2007; Spezio et al., 2008) or laboratory-based simulated election outcomes (Chiao et al., 2008). Here, we replicated this result, finding that both attractiveness and competence judgments predicted the voting choices of HCs in simulated election races between pairs of candidates. Thus, voting decisions in this task rely on a comparison process involving (at least) two attributes.

Patients with LOFC damage were able to make both attractiveness and competence judgments based on the face stimuli, providing ratings that were similar to those made by the control groups. However, these judgments did not predict voting choices in the same way as they did in the control groups. The choices of LOFC patients were not influenced by perceived competence, although perceived attractiveness retained predictive power.

The LOFC has been implicated separately in social evaluations and certain aspects of economic choice. Here, we bring these two streams of research together, providing evidence that this region is necessary for making political choices that consistently relate to multi-attribute social evaluation based on faces. Recent fMRI work has suggested a specific role for this region in the dynamic updating of "first impressions" based on accumulation of information from social observations (Bhanji and Beer, 2013). Activity in a similar area has also been related to trustworthiness assessment based on faces to guide decision-making in an ultimatum game (Kim et al., 2012).

The function of the LOFC has been studied in more detail in the context of reinforcement learning and economic choice. Converging evidence from human fMRI, macaque electrophysiology, and selective lesion experiments argues for distinctions between the medial OFC and LOFC, with the LOFC implicated in value comparison, whereas the medial OFC/vmPFC represents the predicted value of possible outcomes (Rushworth et al., 2012; Rudebeck and Murray, 2014). Our findings can be interpreted as evidence that the LOFC is important in integrating social information to develop a relative preference, although this region is not critical for judging the individual social attributes that contribute to that integration. This is consistent with a previous study showing that OFC damage impaired that ability to incorporate social information (in this case, negative emotional state) inferred from facial expressions when making an overall judgment of "approachability" of people based on photographs of their faces, despite an intact ability to recognize the emotional information conveyed by those stimuli (Willis et al., 2010). It also agrees broadly with the distinction between value representation and value comparison proposed for the medial OFC and LOFC in the reward learning literature.

These results point more specifically to a difficulty in comparing multiple attributes after LOFC damage, with such patients apparently relying on a single, simpler attribute (attractiveness) to solve the decision problem, whereas control groups were capable of incorporating at least two streams of information, including one requiring a social inference. The question of how value is "constructed," i.e., how multiple attributes are combined in decision-making, is an important one that the field is just beginning to consider. Previous lesion work showed that patients with VMF damage approach explicitly multi-attribute decision problems in a way that differed markedly from those with non-VMF frontal damage, perhaps a strategy to reduce the load of comparing across multiple attributes (Fellows, 2006). Recent fMRI and modeling work argues for attribute comparisons at several levels within the brain and also identifies the LOFC as important for resolving competition between stimuli of similar value (Hunt et al., 2014). Additional work will be needed to establish whether the LOFC effect we observed is attributable to difficulties combining attribute information in general or to specific problems with drawing on higher-order social inferences, as opposed to simpler perceptual elements, when making decisions.

Despite the fMRI and animal model evidence that the LOFC and medial OFC make distinct contributions to decision-making, the present study is one of only a few to date attempting to test the specific effects of LOFC damage in humans. This reflects the spatial limitations of human lesion studies in general and the challenges of isolating the LOFC in particular. This region is not commonly injured alone: as seen in the sample studied here, damage to the LOFC is associated typically with either medial OFC/vmPFC damage (e.g., after anterior communicating aneurysm rupture) or ventrolateral prefrontal damage (e.g., after ischemic stroke affecting branches of the middle cerebral artery). As such, most work to date applying region-of-interest designs to

study orbitofrontal damage has either lumped the medial OFC and LOFC together or has split the LOFC-damaged patients into ventromedial frontal and laterofrontal groups, likely diluting or offsetting any specific effects that might be attributable to this region. One recent exception examined the effects of LOFC versus vmPFC lesions on regret and disappointment in risky decision-making, finding differences between these two groups, with LOFC damage associated with less regret and vmPFC damage with more risk-taking (Levens et al., 2014). It is not clear how to link that finding with the current result, given that the present task involved entirely hypothetical choices, making it unlikely that regret considerations played a role in the decision, but at the least this supports the principle that human lesion studies can resolve orbitofrontal damage effects at this finer level of resolution. Voxel-based lesion-symptom mapping studies also provide preliminary support for contributions of both medial and LOFC damage to reinforcement learning (Tsuchida et al., 2010). We note that an unavoidable limitation of all of this work is uncertainty about the contributions of disrupted white matter tracts, including fibers of passage; nonhuman primate lesion studies are needed to definitively address that point (Rudebeck et al., 2013).

The analysis we report here focused a priori on the LOFC using a region-of-interest definition based on existing fMRI work. We also explored the effects of ventromedial frontal damage on the same measures and found similar, although somewhat weaker, patterns with this alternative method of categorizing lesions. A third analysis excluded the LOFC group entirely, contrasting vmPFC-damaged patients to a frontal control group, and found that performance in those two groups did not differ from HCs. These secondary analyses were undertaken *post hoc* and should be interpreted with caution, but together, these results support our a priori hypothesis that the LOFC specifically is involved critically in multi-attribute political choices.

Political science has not necessarily framed decision-making in the context of reward, subjective value, and risk that are typically central to economic models of individual choice (S. Krastev, J. McGuire, D. McNeney, J. Kable, D. Stolle, E. Gidengil, and L.K. Fellows, unpublished observations). Political choice differs in important ways from many economic choices, including its heavy emphasis on collective action: the consequences of a vote potentially affect everyone in a given society, and the political choice itself and its expected benefits also depend on the decisions of other voters. Politics requires citizens to answer difficult and often complex questions (Kuklinski and Quirk, 2000) involving multiple dimensions and other voters' decisions, often in the absence of reliable information. Moreover, politics provides little in the way of useful feedback on the correctness of the choice (Kuklinski and Quirk, 2000), and the motivation and cognitive work required often eclipse the amount of effort most citizens are willing to invest in political affairs (Fiske and Taylor, 1991). Indeed, Downs (1957) argued that most voters are rationally ignorant about politics. Thus, political choice may be particularly likely to reveal how multiple attributes are reconciled and may rely more heavily on simplifying strategies, such as the first-impression judgments studied here.

Despite these differences, there are many reasons to expect that economic and political choices rely at least partly on shared brain substrates. The present study argues that, at least in the very simplified setting of a laboratory election paradigm, political decisions can be predicted by independently generated ratings of relevant attributes, consistent with observations from neuroeconomic paradigms (Armel et al., 2008; Rangel et al., 2008). Furthermore, damage to a specific region within the frontal lobes systematically disrupts a particular component of this process in a way consistent with other cognitive neuroscience evidence implicating this region in value comparison and decision-making in both economic and social contexts.

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